



## Research Article

# Impacts of native and alien plant dominants at different spatial scales

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## Abstract

Plant invasion science has made a substantial progress in documenting the impacts of aliens, but comparisons with the impacts of native dominants are still rare. Further, the impacts on larger spatial scales remain poorly understood. We recorded the impacts of 10 native and nine invasive dominant plants in the Czech Republic on species richness and Shannon diversity by comparing communities with high vs. low cover of the dominant species. To estimate the impacts at the (i) population level and (ii) between-population level, we compared the Jaccard dissimilarity, nestedness and turnover of high- and low-dominance plots. Further, we calculated the Jaccard dissimilarity, nestedness and turnover between the high- and low-dominance plots within each population to express the impacts on species composition. We tested whether (i) native and invasive dominants affect the population- and between population levels of diversity by making the vegetation more homogenous; (ii) whether these effects differ between the native and alien dominants; and (iii) whether the impacts at different spatial levels are related. At the population level, high-dominance plots (with both native and alien dominants) showed higher nestedness and lower turnover compared to the low-dominance plots. Further, all plots with native dominants, both with high- and low dominance, showed higher similarity but lower nestedness than plots with alien dominants. Most importantly, high-dominance plots with native dominants were more similar to each other but showed marginally significantly lower nestedness compared to high-dominance plots with alien dominants. At the between-population level, high-dominance plots with native dominants showed a marginally significantly lower turnover compared to high-dominance plots with alien dominants. The differences in Jaccard dissimilarity, nestedness and turnover between the low- and high-dominance plots at the population level showed strong positive relations to low- and high-dominance differences at the between-populations level. Further, compositional impacts, expressed as the dissimilarity between high- vs. low-dominance plots, positively related to the plot-level impacts on Shannon diversity. Our results show that (i) both native and invasive dominants tend to reduce the diversity over larger areas and that the effect of native dominants may be even stronger, and (ii) the effects on plot-level richness and diversity cannot be easily extrapolated to larger scales but the impacts at the population- and between-populations levels are positively related.



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## Introduction

In the last decades, progress has been made toward documenting the community-level impacts of invasive plants (e.g. Hejda et al. 2009; Vilá et al. 2011; Pyšek et al. 2020), which includes comparisons between the impacts of native vs. alien dominants (Paolucci et al. 2013; Buckley and Catford 2016; Hejda et al. 2017, 2019; Pergl et al. 2023). However, the impacts of native dominants on the species richness and diversity are still rarely studied (but see Pivello et al. 2018; Hejda et al. 2021), even though it can be presumed that their impacts are comparable to that of invasive dominants, given their aggressive spread and high-levels of dominance (e.g. Hejda et al. 2021). In this sense, many natives behave like so-called “super-dominants” (Pivello et al. 2018), with expected strong impacts on species richness, diversity and composition. The association between high levels of dominance and lower species richness has long been established (e.g. Able and Noon 1976) and, at the same time, shifts in dominance are usually apparent earlier than the reduction in species richness, which makes dominance an important indicator of the global change (Chapin et al. 2000). Further, dominant aliens can not only change species richness but also the proportional representation of individual species in the community (Hillebrand et al. 2008). However, how these community-level impacts scale up to larger areas remains mostly unexplored, with the few results so far being rather contradictory (see, e.g. Martin and Wilsey 2015; Dyderski and Jagodzinski 2021). Similarly, previous studies comparing the effects of alien and native dominants have focused on changes in species richness (alpha diversity, e.g. Czarniecka-Wiera et al. 2019), whereas changes in species composition (beta diversity) remain less explored.

There are several ways to define diversity at different spatial scales. A plot-level diversity generally refers to alpha diversity, as it usually represents species richness or diversity measured at scales ranging from 1 m<sup>2</sup> to a few hundred m<sup>2</sup>. The scale of alpha diversity also represents an important issue, as the number of species sampled increases non-linearly with increasing spatial scale (Gotelli and Colwell 2001), which can lead to different shapes of species-accumulation curves. The scale of measuring alpha diversity also represents a challenging issue, as different types of vegetation can have very different shapes of species-accumulation curves (Gotelli and Colwell 2001; Roswell et al. 2021). Further, there is a question on how to define beta diversity or a large -scale diversity in general. A common definition of beta diversity is the variation in species composition amongst distinct sites in a particular geographical location (Whittaker 1960). One approach is to partition the regional gamma diversity into within-alpha diversity and between-beta diversity components.

It is evident that when measuring the effects on alpha diversity, the small-scale (plot-level) effects cannot be easily extrapolated to larger scales (Chase et al. 2018). Further, the changes in plot-level richness (or alpha diversity) provide only a limited view of the changes in diversity, and it is necessary to include information on the spatial changes in species composition (Chase et al. 2018, 2019). For example, changes in composition can happen even without changes in the number of species (e.g. species replacement whilst the total number of species remains equal).

A theoretical paper by Socolar et al. (2016) suggests four basic mechanisms for how beta-diversity may be enlarged or reduced: (i) additive heterogenization, when locally specific species are added; (ii) additive homogenization, when common



and spatially unspecific species are added; (iii) subtractive heterogenization, when common species disappear, become rare or locally specific; and (iv) subtractive homogenization, when rare or locally specific species disappear. It is most likely the interplay of all these effects that drive changes in large-scale diversity patterns. However, it can be presumed that the mechanism of “subtractive homogenization” plays a major role, as the dominant plants are documented to reduce local species richness and diversity (e.g. Hejda et al. 2021).

The case studies focused on the role of dominant species provide contradictory results and show that native dominant species can result in stronger biotic homogenization than aliens (Dyderski and Jagodziński 2021). Schlegel and Riesen (2021) reported that the native dominant *Pteridium aquilinum* suppressed the alpha diversity and eliminated the Red-Listed species of Orthoptera but, at the same time, increased beta diversity over large scales. On the contrary, Fukami et al. (2013) documented that alien dominants prevented the vegetation from diverging during succession, reducing riparian vegetation’s beta diversity. Martin and Wilsey (2015) showed that the diversity of native- vs. alien-dominated grasslands differed along a north-south gradient (from Minnesota to Texas, USA) with regard to the spatial scale. The local diversity was consistently higher in native-dominated grasslands, and regional diversity was higher in the native-dominated grasslands in the north of the area studied, while alien-dominated grasslands had higher diversity in the south, and the diversity of the alien-dominated grassland was generally greater across the whole area. The authors suggested several mechanisms to interpret this somewhat surprising pattern, including present and past patchiness and inter-patch connectivity, disturbance history, or present and past management (Martin and Wilsey 2015).

This paper aims to address these issues by analysing plant community data sampled across the Czech Republic, central Europe. In particular, we aim to test the following questions: (i) Do the local, plot-level impacts of native and alien dominants on species richness and diversity scale up to the within- and across-population levels (ii) Do these effects differ between the native and invasive alien dominants? (iii) Are the effects of dominants recorded at different spatial scales related or independent?

## Methods

### Sampling design

We sampled populations of 10 native (*Calamagrostis epigejos*, *Cirsium arvense*, *Cirsium heterophyllum*, *Cirsium oleraceum*, *Filipendula ulmaria*, *Petasites hybridus*, *Phalaris arundinacea*, *Rubus idaeus*, *Tanacetum vulgare*, and *Urtica dioica*) and nine invasive dominant plants (*Aster novi-belgii* agg., *Heracleum mantegazzianum*, *Impatiens glandulifera*, *Lupinus polyphyllus*, *Reynoutria japonica*, *Reynoutria ×bohemica*, *Rumex alpinus*, *Solidago canadensis*, and *Telekia speciosa*; Suppl. material 1). We sampled plots of 4 × 4 m in size located within populations of studied species across the Czech Republic (Suppl. material 2) that ranged from hundreds to thousands of m<sup>2</sup> in size (see Hejda et al. 2021 for details on the sampling scheme); the populations were selected so as to include stands with high and low dominance of the target dominant species. Low dominance referred to 0–25% cover of the target species, and these low-cover plots were used as controls. On the contrary,



high dominance encompassed >50% of the dominant species cover (see Hejda et al. 2021 for details). We then estimated the local impacts of these dominant species on species richness and Shannon diversity index of invaded communities, as well as on species composition.

## Diversity measure

To detect the changes in species composition associated with the dominant species, we calculated the Jaccard dissimilarity index, which is based on incidence data (Jaccard 1900) and regarded as robust to taxonomic error as well as both numerical and geographical undersampling (Schroeder and Jenkins 2018).

We calculated the Jaccard dissimilarity index ( $\beta_{jac}$ ) at the (i) population-level (= dissimilarity of plots within populations); and (ii) between-population level (= dissimilarity of plots between populations), using the `beta.pair` function (index.family="jaccard") of the `betapart` package (Baselga 2013; R Core Team 2022). The values of the index range from 0 (maximum similarity or lowest dissimilarity) to 1 (minimum similarity or highest dissimilarity). The following formula was used:

$$\beta_{jac} = \frac{b+c}{a+b+c}$$

where  $a$  is the number of species in common between two sites,  $b$  is the number of species unique to the site with the lowest number of species, and  $c$  the number of species unique to the site with the largest number of species.

Total Jaccard can be partitioned into turnover ( $\beta_{jtu}$ ) and nestedness component ( $\beta_{jne}$ ):

$$\beta_{jac} = \beta_{jtu} + \beta_{jne} = \frac{2b}{(2b+a)} + \left( \frac{c-b}{a+b+c} \right) \left( \frac{a}{2b+a} \right)$$

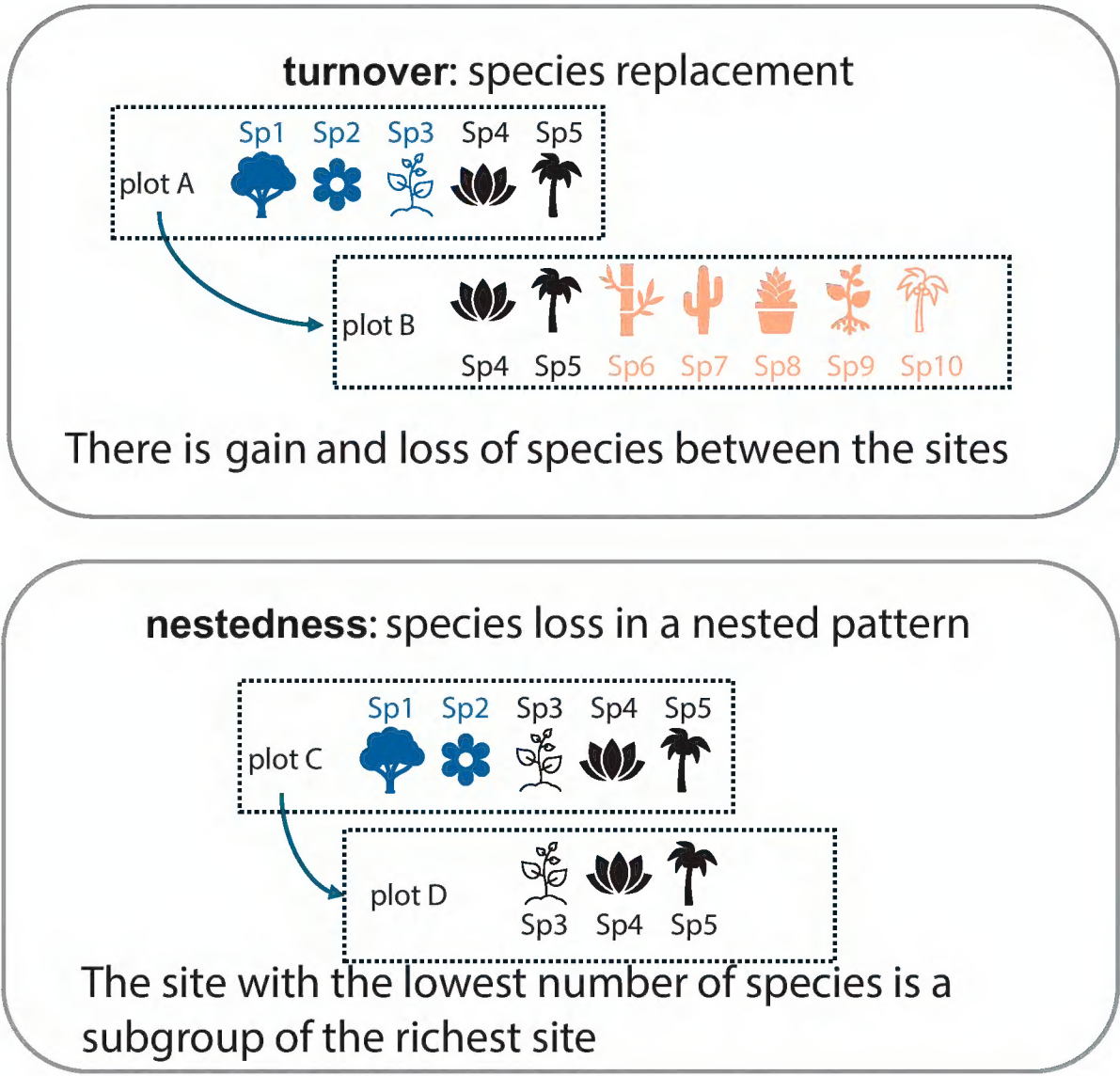
Nestedness refers to changes in species richness, in which the site with the lowest richness represents a subset of species of the richest site, and turnover, which refers to species replacement from site to site (Baselga and Orme 2012) (see Fig. 1 for a schematic representation of turnover and nestedness).

We estimated the population- and between-population level impacts as differences in similarity between the plots with low vs. high dominance of the selected dominants, assuming that this represents the homogenizing effect of the dominant species (see Fig. 2 for a schematic representation of our sampling design and how the diversity metrics were calculated at distinct spatial scales).

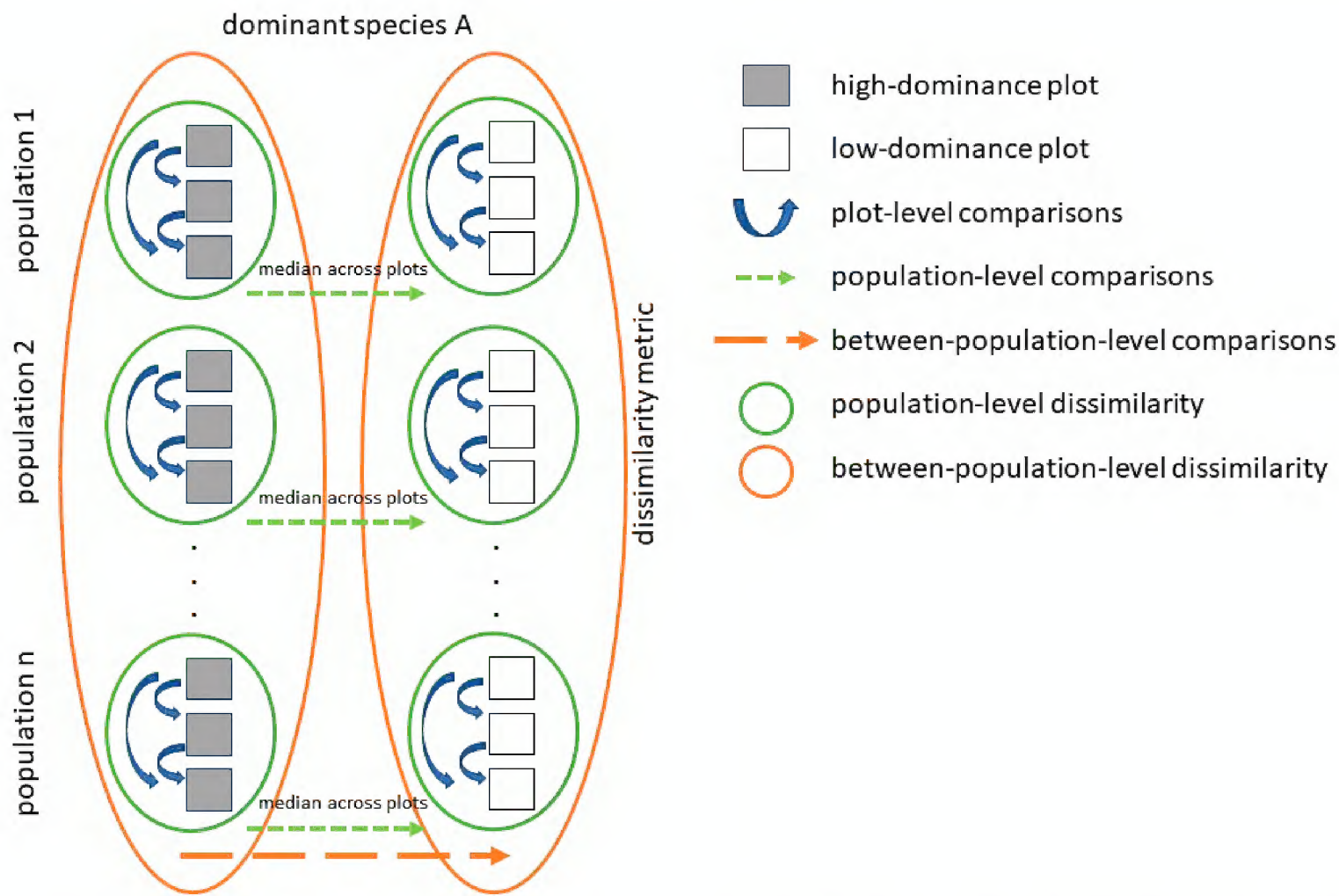
At the population level, we calculated Jaccard, turnover and nestedness amongst all high-dominance plots and amongst all low-dominance plots to each population of each species. We then recorded the median value in each population with high-dominance plots and compared them with the corresponding median values of the low-dominance plots.

Further, we compared the total Jaccard, nestedness and turnover of high-dominance plots with native vs. alien dominants to compare their homogenizing effect. In the case of the population-level impacts, we also calculated the Jaccard dissimilarity, nestedness and turnover between the high- and low-dominance plots within each population to express the population-level impact on species composition, assuming that the lower similarity between the low and high dominance plots (within populations) shows a larger impact on species composition. Here, to tackle the challenge of





**Figure 1.** Schematic representation of the partitioning of the Jaccard dissimilarity index into turnover and nestedness components (see text for the formula and more information). Turnover refers to the gain and loss of species (species replacement) between the areas (e.g. high dominance plots of a particular dominant species), whereas nestedness refers to the cases where the plot with the lowest number of species represents a subgroup of species of the richest plot/site. In the scheme, the species in blue are unique to plots A and C, the species in black are shared between both plots and the species in orange are unique to plot B.



**Figure 2.** Scheme of our sampling design and how the impacts were estimated. The plot level is marked with blue arrows, the population level is marked with dashed green arrows, and the between-population level with the dashed orange arrows. In each population, the median value across all high-dominance plots and the median value across all low-dominance plots were computed; these median values of high and low-dominance plots were then compared in the analyses.



comparing different numbers of high and low dominance plots, given that the high vs low combination itself is substantially higher than high vs. high and low vs. low, we combined all high-dominance plots of a population as a single “high dominance plot”, and similarly for a single “low dominance plot”. Thus, in each population of each species, we recorded a single direct dissimilarity distance of high vs. low-dominance plots.

To express the plot-level impacts, we used LMM regression models to relate the plot-level species richness and Shannon diversity to the cover of selected dominants, accounting for the identity of dominant species and their populations (nested in “dominants”) by setting these as random effects. We quantified the plot-level impacts as the slope/intercept ratios of the corresponding LMM regression models, accounting for the a priori different species richness and diversity of different types of vegetation (see Hejda et al. 2021 for details on data processing and analyses).

Further, we used LMM models to compare the similarity, nestedness and turnover of low- vs. high-dominance plots at the population- and between-population levels and the effects of native vs. alien invasive dominants. Further, we used parametric and non-parametric correlations to test the relationships between the effects at different spatial levels.

## Results

### Impacts at the population level

At the population level, high-dominance plots with both native and alien dominants taken together showed higher nestedness and lower turnover compared to all low-dominance plots ( $p = 0.018$  and  $p = 0.002$ , resp.). In other words, sites with high dominance were linked to a higher degree of nestedness (which in turn is related to species losses), consistently for both alien and native dominants (see Table 1).

Considering all plots with native dominants (high and low dominance plots taken together) vs. all plots with alien dominants, we found that the former were more similar to each other but also had a lower nestedness than plots with alien dominants ( $p = 0.039$  and  $p = 0.043$ , respectively, Table 2, see also Suppl. material 3 for the details on statistical tests).

Comparing high-dominance plots with native and alien dominants, we found that the former showed lower Jaccard dissimilarity (i.e., were more similar), whereas the latter had marginally significantly higher nestedness ( $p = 0.045$  and  $p = 0.072$ , resp.). In other words, plots with a high native dominance had more species in common than plots with a high dominance of aliens, where the species loss was stronger.

Considering the low-dominance plots, no significant differences in Jaccard, nestedness or turnover were detected between native and alien dominants. At the population level, no significant differences between the effects of native vs. alien dominants (defined as differences in dissimilarity, nestedness and turnover between the low- and high-dominance plots) were found (Table 1).

### Impacts at the between-population level

High-dominance plots with alien dominants showed higher species turnover compared to high-dominance plots with native dominants, but this difference is only marginally significant ( $p = 0.051$ , Table 2). Comparing high and low-dominance plots within the same origin of dominants, native dominants show lower levels



**Table 1.** Jaccard dissimilarity, nestedness and turnover values as recorded at the population level. Each consecutive line represents the comparison being made (e.g. high and low plot dominance of all dominants taken together). Values differing significantly are in **bold** ( $p<0.05$ ), values differing marginally significantly are in *italics* ( $p<0.1$ ). Please see the Suppl. material 3 for more details on statistical models.

Origin of the dominant species	plot dominance	Jaccard dissimilarity	S.D.	nestedness	S.D.	turnover	S.D.
native and alien	high	0.306	0.233	<b>0.048</b>	0.07	<b>0.213</b>	0.205
native and alien	low	0.347	0.261	<b>0.029</b>	0.04	<b>0.302</b>	0.241
native	high and low	<b>0.284</b>	0.233	<b>0.034</b>	0.05	0.227	0.214
alien	high and low	<b>0.374</b>	0.255	<b>0.045</b>	0.065	0.291	0.238
native	high	<b>0.267</b>	0.216	<i>0.04</i>	0.06	0.19	0.192
alien	high	<b>0.35</b>	0.244	<i>0.058</i>	0.079	0.238	0.217
native	low	0.299	0.25	0.027	0.035	0.261	0.229
alien	low	0.399	0.266	0.031	0.044	0.344	0.248
native	low v high	0.033	0.34	-0.013	0.072	0.073	0.316
alien	low v high	0.049	0.386	-0.027	0.081	0.106	0.344

**Table 2.** Jaccard dissimilarity, nestedness and turnover values as recorded at the between-population-level. Values differing marginally significantly are in *italics*. Please see the Suppl. material 3 for more details on statistical models.

Origin of the dominant species	plot dominance	Jaccard dissimilarity	S.D.	nestedness	S.D.	turnover	S.D.
native and alien	high	0.296	0.126	0.032	0.035	0.194	0.114
native and alien	low	0.357	0.146	0.015	0.011	0.311	0.153
native	high and low	0.287	0.083	0.022	0.033	0.21	0.123
alien	high and low	0.371	0.172	0.025	0.02	0.299	0.159
native	high	0.263	0.035	0.03	0.045	<i>0.146</i>	0.082
alien	high	0.333	0.177	0.034	0.024	<i>0.247</i>	0.125
native	low	0.311	0.11	0.015	0.012	0.275	0.126
alien	low	0.408	0.169	0.016	0.01	0.35	0.178
native	low v high	-0.049	0.111	0.014	0.047	-0.129	0.186
alien	low v high	-0.074	0.334	0.019	0.024	-0.103	0.286

of turnover in high-dominance plots compared to low-dominance plots, whereas alien dominants show higher levels of nestedness in high-dominance plots compared to low-dominance plots (Fig. 3). Similarly to the population level, no differences in the effects of native vs. invasive dominants, defined as the dissimilarity differences between the low- and high-dominance plots, were detected at the between-population level (Table 2).

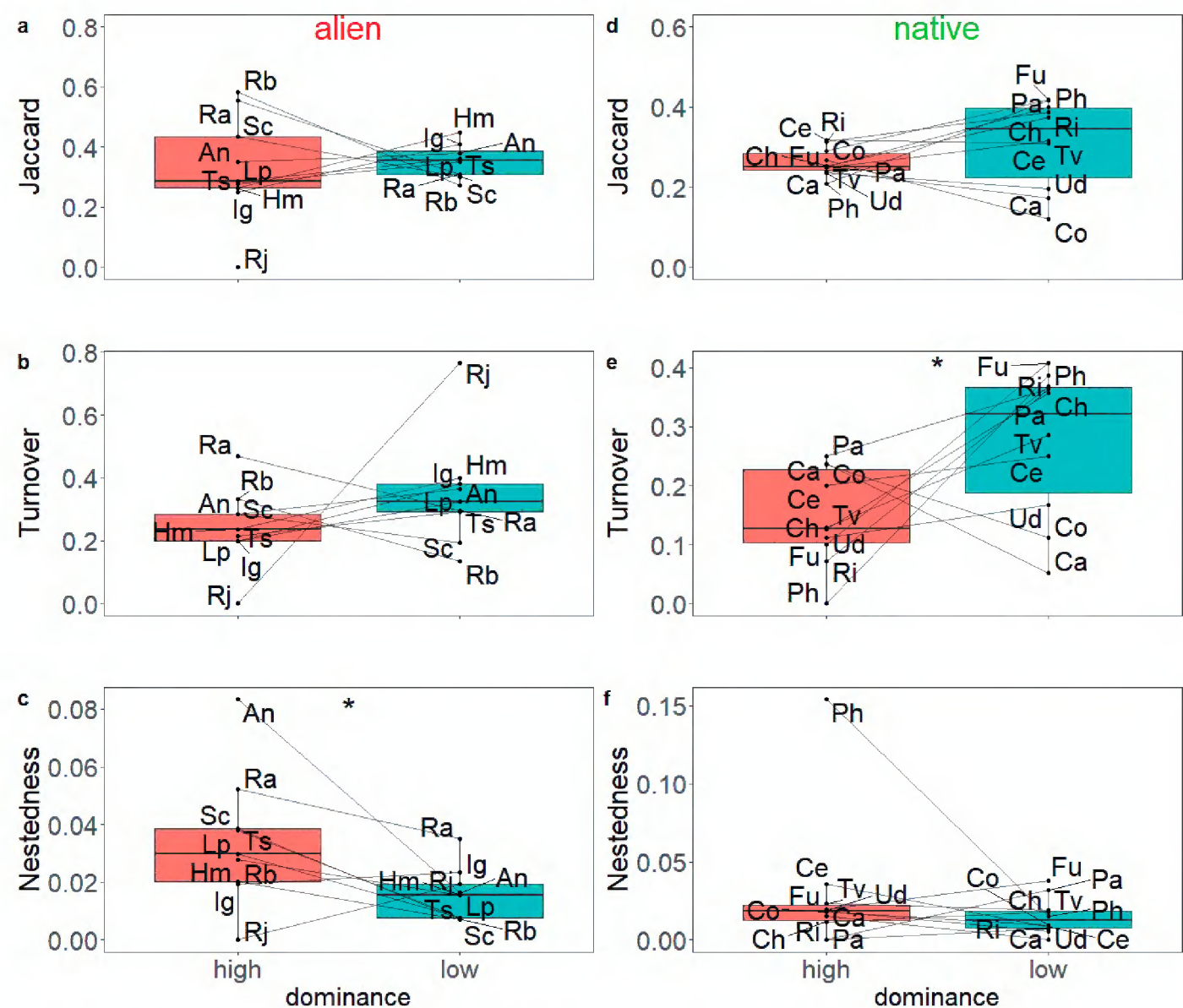
**Relations between the impacts at different spatial scales**

No significant relationships between the impacts recorded at the plot- and either population- or between-population levels were detected (Table 3). On the contrary, strong positive relationships between the population- and between-population level impacts were found for Jaccard dissimilarity, nestedness and turnover (Table 3). These strongly significant positive relationships were identified using both parametric (Pearson) and non-parametric correlations (Spearman, Kendall; see Suppl. material 3 for the results of non-parametric correlations).



**Table 3.** Relations between the impacts at different spatial levels for alien and native dominants taken together. The impacts at the plot-level are defined as the slope/intercept ratios of regression models relating the plot-level richness or Shannon diversity to the cover of the target dominant. The impacts at the population and between-population levels are defined as differences in dissimilarity between the high- and low-dominance plots. Significant relations are in bold. Please see the Suppl. material 3 for more details on statistical models.

spatial level I	spatial level II	measure I	measure II	Pearson correlation	p-value
plot	population	species richness	Jaccard dissimilarity	0.283	0.24
plot	population	Shannon diversity	Jaccard dissimilarity	0.123	0.616
plot	population	species richness	nestedness	0.03	0.904
plot	population	Shannon diversity	nestedness	-0.052	0.833
plot	population	species richness	turnover	-0.259	0.285
plot	population	Shannon diversity	turnover	-0.093	0.704
plot	between-population	species richness	Jaccard dissimilarity	-0.172	0.483
plot	between-population	Shannon diversity	Jaccard dissimilarity	-0.085	0.73
plot	between-population	species richness	nestedness	0.074	0.763
plot	between-population	Shannon diversity	nestedness	0.092	0.707
plot	between-population	species richness	turnover	-0.171	0.483
plot	between-population	Shannon diversity	turnover	-0.075	0.761
population	between-population	Jaccard dissimilarity	Jaccard dissimilarity	<b>0.963</b>	<b>p&lt;0.001</b>
population	between-population	nestedness	nestedness	<b>0.777</b>	<b>p&lt;0.001</b>
population	between-population	turnover	turnover	<b>0.911</b>	<b>p&lt;0.001</b>



**Figure 3.** Between-population level results for all species. Each dot represents the median value across all sites of the same species at a certain dominance category (high or low); each line connects the dominance category of a species. Alien dominants (a-c) show higher levels of nestedness in high-dominance plots compared to low-dominance plots, whereas native dominants (d-f) show lower levels of turnover in high-dominance plots compared to low-dominance plots. Alien species: An: *Aster novi-belgii* agg., Hm: *Heracleum mantegazzianum*, Ig: *Impatiens glandulifera*, Lp: *Lupinus polyphyllus*, Rj: *Reynoutria japonica*, Rb: *Reynoutria ×bohemica*, Ra: *Rumex alpinus*, Sc: *Solidago canadensis*, Ts: *Telekia speciosa*; native species: Ce: *Calamagrostis epigejos*, Ca: *Cirsium arvense*, Ch: *Cirsium heterophyllum*, Co: *Cirsium oleraceum*, Fu: *Filipendula ulmaria*, Ph: *Petasites hybridus*, Pa: *Phalaris arundinacea*, Ri: *Rubus idaeus*, Tv: *Tanacetum vulgare*, Ud: *Urtica dioica*.



We found strong positive relationships between the plot-level impacts on Shannon diversity and population-level impacts on species composition, expressed as the similarity between the low- and high-dominance plots within each population (Table 4). We also detected a strong negative relation between the turnover at the population level (the turnover component of the population-level compositional impacts) and the impacts on the turnover of species at the between-population level (expressed as the differences in turnover between the low- and high-dominance plots). Similarly to the previous finding, the relationship between the turnover component of the population-level compositional impacts and the turnover component of the between-population-level impacts was significant when both parametric (Pearson correlation) and non-parametric methods (Spearman and Kendal correlation; see Suppl. material 3) were used.

Discussion

Impacts at the population level

At the population level, high-dominance plots show higher nestedness and lower turnover than low-dominance plots. In other words, taking alien and native species together, the high-dominance plots lose more species in a nested pattern, and the species replacement is lower than in the low-dominance plots. However,

**Table 4.** Relations between impacts at the plot-, population- and between-population-levels and compositional impacts at the population-level. These refer to the direct low v. high dominance comparison. The impacts at the plot-level are defined as the slope/intercept ratios of regression models relating the plot-level richness or Shannon diversity to the cover of the target dominant. The impacts at the population and between-population levels are defined as differences in dissimilarity between the high- and low-dominance plots. Compositional impacts at the population level are defined as the dissimilarity between the low- and high-dominance plots within each population. Please see the Suppl. material 3 for more details on statistical models.

Comparison group	level I	level II	impact I	impact II	Correlation
A	population-level	plot-level (species richness)	low-high dissimilarity (Jaccard dissimilarity)	slope/intercept ratios	0.45 (p = 0.053)
A	population-level	plot-level (species richness)	low-high dissimilarity (nestedness)	slope/intercept ratios	
A	population-level	plot-level (species richness)	low-high dissimilarity (turnover)	slope/intercept ratios	
A	population-level	plot-level (Shannon diversity)	low-high dissimilarity (Jaccard dissimilarity)	slope/intercept ratios	0.586 (p = 0.008)
A	population-level	plot-level (Shannon diversity)	low-high dissimilarity (nestedness)	slope/intercept ratios	
A	population-level	plot-level (Shannon diversity)	low-high dissimilarity (turnover)	slope/intercept ratios	
B	population-level	population-level	low-high dissimilarity (Jaccard dissimilarity)	low-high differences (Jaccard dissimilarity)	
B	population-level	population-level	low-high dissimilarity (nestedness)	low-high differences (nestedness)	
B	population-level	population-level	low-high dissimilarity (turnover)	low-high differences (turnover)	
C	population-level	between-population-level	low-high dissimilarity (Jaccard dissimilarity)	low-high differences (Jaccard dissimilarity)	
C	population-level	between-population-level	low-high dissimilarity (nestedness)	low-high differences (nestedness)	
C	population-level	between-population-level	low-high dissimilarity (turnover)	low-high differences (turnover)	-0.530 (p = 0.02)



no significant difference in Jaccard dissimilarity between the low- and high-dominance plots was recorded at the population level, suggesting that the high-dominance plots are not necessarily less diverse and more homogenous than the adjacent low-dominance plots. Apparently, distinctive dominants can lower the local, plot-level (alpha) diversity without affecting the large-scale diversity expressed by the beta diversity indices. However, Kortz and Magurran (2019) found a contrasting pattern: the presence of aliens was associated with an increase in the local diversity, as areas with more aliens tend to have more species, but decreased the large-scale (beta) diversity, by making the vegetation more homogenous due to adding commonly shared aliens amongst the areas. A similar pattern was detected by Nobis et al. (2016): the local richness of native and alien species was positively related. However, the richness of alien species was negatively related to native beta and gamma diversity, which especially concerned red-listed species. Importantly, the fact that aliens contribute to plot-level diversity precludes the competitive exclusion of native species by dominant aliens.

The homogenizing effect of alien dominants was described for some aliens, such as the amphibious *Althernanthera philoxeroides* (Wu et al. 2022). The large-scale impacts of this species were context-dependent, being stronger in invaded terrestrial rather than aquatic habitats and in the northern part of the invaded range in China. In other cases, the effects of invasive aliens on native diversity were detected to be consistently negative across different spatial scales. For example, Stotz et al. (2019) detected a consistently negative effect of the invasive *Bromus inermis* both within and across individual grasslands in Alberta, Canada, and Boscutti et al. (2020) detected a spatially consistent negative effect of the invasive *Amorpha fruticosa* in northern Italy. Interestingly, Bando et al. (2022) detected a negative effect of the invasive *Urochloa arrecta* on both spatial and temporal beta-diversity in Brazil.

We did not find studies comparing the large-scale effects of multiple invasive and native dominants, even though there are studies comparing the large-scale impacts of invasive aliens in their native and invaded ranges – see for example Lolis et al. (2019), who detected a negative effect of the invasive *Eichhornia crassipes* on both alpha and beta diversity in the invaded range, China, but not in its native range, Brazil.

When comparing plots with high dominance of native species with those of aliens, the former were more similar (i.e., showed lower dissimilarity), pointing to their stronger homogenizing effect. At the same time, high-dominance plots with native dominants also showed marginally lower nestedness than their alien counterparts. The same pattern was detected for all plots merged regardless of the degree of dominance: those with native dominants are more similar but show lower nestedness than plots with alien dominants.

### Impacts at the between-population level

It needs to be stressed that the tests on the differences between high- and low-dominance plots, as well as between the native vs. alien dominants at the between-population level, are weak due to the high residual variability. This is because the data include samples with different dominants, both native and alien, and with different types of vegetation, both within- and across dominants. Inevitably, this introduces a lot of residual variability that remains unexplained by our models.



No significant differences between the low- and high-dominance plots and between the native and alien dominants were recorded at the between-population level, except that high-dominance plots with native dominants showed a marginally significantly lower species turnover. This again suggests a slightly stronger homogenizing effect of native dominants, similar to that recorded at the population level. This is also in line with recent evidence that areas across the globe with alien plants have higher levels of species replacement than areas with native species only (Kortz et al. 2023).

### **Relationship between the impacts of dominant species recorded at different spatial scales**

When the population and between-population-level impacts were defined as differences in Jaccard similarity, nestedness, and turnover between the low- and high-dominance plots, no significant relationships between the impacts recorded at the plot level and those measured at either the population or between-population levels were revealed. However, we recorded strong positive relationships between the impacts at the population- and between-population levels, and this holds for all three indices used, i.e., Jaccard dissimilarity, nestedness and turnover. This clearly shows that the impacts at the population- and between-population levels are strongly related; however, it also confirms that plot-level impacts cannot be easily extrapolated to higher spatial scales.

On the contrary, we recorded strong positive relations between the plot-level impacts on Shannon diversity and the population-level impacts on species composition. This indicates that changes in the plot-level alpha diversity are strongly associated with compositional changes. Further, the turnover component of the population-level compositional impacts was strongly negatively related to the turnover component of the between-population-level impacts, defined as the differences between the low- and high-dominance plots.

### **Conclusions**

Our results suggest that the homogenizing effects of native dominants are equal to or even stronger than those of the invasive alien dominants, which concerns the impacts recorded at the population- and partially also at the between-population levels.

Our results also support the assertion that the plot-level impacts on neither species richness nor Shannon diversity can be easily extrapolated to higher spatial levels. However, the plot-level impacts on Shannon diversity relate to the compositional impacts recorded at the population level, and the impacts recorded at the population- and between-population levels are also positively associated.

These results suggest that conservation efforts aiming at the maintenance of the diversity of communities and landscapes should target not only invasive aliens but also native expansive species with dominant tendencies. This is especially true in Eurasia or the Old World in general, with an array of native synanthropic dominants with expansive tendencies. However, the situation may be completely different in areas without a long tradition of a strong human impact (New World, distant islands, and archipelagos), which may be, therefore, presumed to lack native dominants with synanthropic tendencies.



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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: AK, MH, JP, PPy. Data curation: MH, AK. Formal analysis: AK, MH. Funding acquisition: JP, PPy. Field work: JS, JP, JK. Methodology: AK, MH, JP, PPy. Project administration: JP. Supervision: PPy. Validation: PPy, AK, JP. Visualization: AK, JP. Writing - original draft: MH, AK. Writing - review and editing: AK, MH, JP, JK, PPe, JS, MVi, MVo, PPy.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

## References

- Able KP, Noon BR (1976) Avian community structure along elevational gradients in the northeastern United States. *Oecologia* 26(3): 275–294. <https://doi.org/10.1007/BF00345296>
- Bando FM, Figueiredo BMS, Moi DA, Thomas SM, Michelan TS, García-Girón J, Heino J, Alahuhta J, Romero GQ, Mormul RP (2022) Invasion by an exotic grass species homogenizes native freshwater plant communities. *Journal of Ecology* 111(4): 799–813. <https://doi.org/10.1111/1365-2745.14061>



- Baselga A (2013) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography* 36(2): 124–128. <https://doi.org/10.1111/j.1600-0587.2012.00124.x>
- Baselga A, Orme CDL (2012) Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution* 3(5): 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Boscutti F, Pellegrini E, Casolo V, de Nobili V, Buccheri M, Alberti G (2020) Cascading effects from plant to soil elucidate how the invasive *Amorpha fruticosa* L. impacts dry grasslands. *Journal of Vegetation Science* 31(4): 667–677. <https://doi.org/10.1111/jvs.12879>
- Buckley YM, Catford J (2016) Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology* 104(1): 4–17. <https://doi.org/10.1111/1365-2745.12501>
- Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S (2000) Consequences of changing biodiversity. *Nature* 405(6783): 234–242. <https://doi.org/10.1038/35012241>
- Chase JM, McGill BJ, McGlinn DJ, May F, Blowes SA, Xiao X, Knight TM, Purschke O, Gotelli NJ (2018) Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecology Letters* 21(11): 1737–1751. <https://doi.org/10.1111/ele.13151>
- Chase JM, McGill BJ, Thompson PL, Antão LH, Bates AE, Blowes SA, Dornelas M, Gonzalez A, Magurran AE, Supp SR, Winter M, Bjorkman AD, Bruelheide H, Byrnes JEK, Cabral JS, Elahi R, Gomez C, Guzman HM, Isbell F, Myers-Smith IH, Jones HP, Hines J, Vellend M, Waldock C, O'Connor M (2019) Species richness change across spatial scales. *Oikos* 128(8): 1079–1091. <https://doi.org/10.1111/oik.05968>
- Czarniecka-Wiera M, Kaćki Z, Chytrý M, Palpurina S (2019) Diversity loss in grasslands due to the increasing dominance of alien and native competitive herbs. *Biodiversity and Conservation* 28(11): 2781–2796. <https://doi.org/10.1007/s10531-019-01794-9>
- Dyderski MK, Jagodziński AM (2021) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. *Biological Invasions* 23(1): 235–252. <https://doi.org/10.1007/s10530-020-02367-6>
- Fukami T, Bellingham BJ, Peltzer DA, Walker LR (2013) Non-native plants disrupt dual promotion of native alpha and beta diversity. *Folia Geobotanica* 48(3): 319–333. <https://doi.org/10.1007/s12224-013-9175-z>
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4(4): 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97(3): 393–403. <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Hejda M, Štajerová K, Pyšek P (2017) Dominance has a biogeographical component: Do plants tend to exert stronger impacts in their invaded rather than native range? *Journal of Biogeography* 44(1): 18–27. <https://doi.org/10.1111/jbi.12801>
- Hejda M, Štajerová K, Pergl J, Pyšek P (2019) Impacts of dominant plant species on trait composition of communities: Comparison between the native and invaded ranges. *Ecosphere* 10(10): e02880. <https://doi.org/10.1002/ecs2.2880>
- Hejda M, Sádlo J, Kutlvašr J, Petřík P, Vítková M, Vojík M, Pyšek P, Pergl J (2021) Impact of invasive and native dominants on species richness and diversity of plant communities. *Preslia* 93(3): 181–201. <https://doi.org/10.23855/preslia.2021.181>
- Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology* 89(6): 1510–1520. <https://doi.org/10.1890/07-1053.1>



- Jaccard P (1900) Contribution au problème de l'immigration post-glaciaire de la flore alpine: Étude comparative de la flore alpine du massif de Wildhorn, du haut bassin du Trient et de la haute vallée de Bagnes. *Bulletin de la Société Vaudoise des Sciences Naturelles* 36: 87–130.
- Kortz A, Magurran AE (2019) Increases in local richness (α-diversity) following invasion are offset by biotic homogenization in a biodiversity hotspot. *Biology Letters* 15(5): 20190133. <https://doi.org/10.1098/rsbl.2019.0133>
- Kortz AR, Moyes F, Pivello VR, Pyšek P, Dornelas M, Visconti P, Magurran AE (2023) Elevated compositional change in plant assemblages linked to invasion. *Proceedings. Biological Sciences* 290(1998): 20222450. <https://doi.org/10.1098/rspb.2022.2450>
- Lolis LA, Alves DC, Fan S, Lv T, Yang L, Li Y, Liu C, Yu D, Thomas SM (2019) Negative correlations between native macrophyte diversity and water hyacinth abundance are stronger in its introduced than in its native range. *Diversity & Distributions* 26(2): 242–253. <https://doi.org/10.1111/ddi.13014>
- Martin LM, Wilsey BJ (2015) Differences in beta diversity between exotic and native grasslands vary with scale along a latitudinal gradient. *Ecology* 96(4): 1042–1051. <https://doi.org/10.1890/14-0772.1>
- Nobis A, Zmihorski M, Kotowksa D (2016) Linking the diversity of native flora to land cover heterogeneity and plant invasions in a river valley. *Biological Conservation* 203: 17–24. <https://doi.org/10.1016/j.biocon.2016.08.032>
- Paolucci EM, MacIsaac HJ, Ricciardi A (2013) Origin matters: Alien consumers inflict greater damage on prey populations than do native consumers. *Diversity & Distributions* 19(8): 988–955. <https://doi.org/10.1111/ddi.12073>
- Pergl J, Vítková M, Hejda M, Kutlvašr J, Petřík P, Sádlo J, Vojík M, Dvořáčková Š, Fleischhans R, Lučanová A, Pyšek P (2023) Plant-soil interactions in the communities dominated by alien and native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 59: 125721. <https://doi.org/10.1016/j.ppees.2023.125721>
- Pivello VR, Vieira MV, Grombone-Guaratini MT, Silva Matos DM (2018) Thinking about super-dominant populations of native species – Examples from Brazil. *Perspectives in Ecology and Conservation* 16(2): 74–82. <https://doi.org/10.1016/j.pecon.2018.04.001>
- Pyšek P, Bacher S, Kühn I, Novoa A, Catford J, Hulme PE, Pergl J, Richardson DM, Wilson JR, Blackburn TM (2020) MAcroecological Framework for Invasive Aliens (MAFIA): Disentangling largescale context-dependence in biological invasions. *NeoBiota* 62: 407–461. <https://doi.org/10.3897/neobiota.62.52787>
- R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.r-project.org/>
- Roswell M, Dushoff J, Winfree R (2021) A conceptual guide to measuring species diversity. *Oikos* 130(3): 321–338. <https://doi.org/10.1111/oik.07202>
- Schlegel J, Riesen M (2021) Bracken fern (*Pteridium aquilinum* (L.) Kuhn) overgrowth on dry Alpine grassland impedes Red List Orthoptera but supports local orthopteran beta diversity. *Journal of Insect Conservation* 25(4): 657–669. <https://doi.org/10.1007/s10841-021-00333-8>
- Schroeder PJ, Jenkins DG (2018) How robust are popular beta diversity indices to sampling error? *Ecosphere* 9(2): e02100. <https://doi.org/10.1002/ecs2.2100>
- Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution* 31(1): 67–80. <https://doi.org/10.1016/j.tree.2015.11.005>
- Stotz GC, Gianioli E, Cahili Jr JF (2019) Biotic homogenization within and across eight widely distributed grasslands following invasion by *Bromus inermis*. *Ecology* 100(7): e02717. <https://doi.org/10.1002/ecy.2717>



- Vilá M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: A meta- analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14(7): 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Whittaker R (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs* 30(3): 279–338. <https://doi.org/10.2307/1943563>
- Wu H, Dong S, Rao B (2022) Latitudinal trends in the structure, similarity and beta diversity of plant communities invaded by *Alternanthera philoxeroides* in heterogeneous habitats. *Frontiers in Plant Science* 13: 1021337. <https://doi.org/10.3389/fpls.2022.1021337>

## Supplementary material 1

### The selected native and invasive dominants

Authors: Alessandra Kortz, Martin Hejda, Jan Pergl, Jiří Sádlo, Josef Kutlvašr, Petr Petřík, Martin Vojík, Michaela Vítková, Petr Pyšek

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## Supplementary material 2

### Map with populations of the selected native and alien dominants

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## Supplementary material 3

### Primary data, details on the statistical models and summary of the results

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